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Optimization of Source-Sink Relationships Based on a Plant Functional-Structural Model: A Case Study on Maize

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Abstract

Based on a functional-structural plant model - GreenLab, the source-sink relationships were investigated in order to analyze the impact of fruit sink strength on the plant biomass production and partition for an optimal yield in the case of maize. The fruit sink strength optimization comes from the fact that there is competition between the fruit and the leaves in demand of biomass according to the results of GreenLab model calibration. A theoretically optimal fruit sink strength value was therefore acquired by solving a bound-constrained optimization problem to act as an evaluation criterion for the species of maize growing in the field, and we name the optimal value fruit sink reference. The optimization results hold with fruit weight serving as the objective function for the bound-constrained optimization problem. According to the fruit sink reference we can tell the maize in the field is the optimal one or not in the sense of GreenLab plant functional-structural characteristics, and possible instructions for hybridization were drawn.

Keywords: plant functional-structural model, GreenLab, sink strength, fruit sink reference, bound-constrained optimization problem

1 Introduction

Over the last decades, plant structure and growth have been simulated by variety of models ranging from morphogenetic program to process-based ecophysiological knowledge[1]. The preliminary plant modeling work was started by Prof. De Wit on photosynthesis activity simulation[2], then decades of efforts spread the studies on plant growth interacting with soils, climate, pests, diseases and weeds. An overall description of plant production system can therefore be obtained. Among these abundant models, GreenLab, one of the plant functional-structural models, contributes to the attempt to merge plant architectural information and its functioning[3].

Based on the plant models, plant biomass can be predicted; plant optimizations are possible. The characteristic of model-based plant optimization relies on the objectives and characteristics of the plant models. For instance, based on AMAPhydro model, optimal rhythmical pruning of fruit for optimal fruit size was obtained in theory[4]; Seginer and

Ioslovich simplified TOMGRO model to introduce optimal control policy when the crop switches between certain growth stages[5].

The objective of GreenLab is to build a plant mathematical engine which simulates the phenotypic plasticity of a genotype, as elucidates the plant growth interacting with environment, say soil, light and temperature. Two biological laws form the temporal and spatial characteristics of GreenLab. One is that organ productions are proportional to the sum of temperatures, which determines that the time step of the dynamical plant model is growth cycle (GC) — the biological thermal time index. The model variables are consequently the fresh weights and geometric sizes of plant at organ level. The other is that biomass production is linearly correlated with water transpiration, which enables GreenLab process hydraulic calculation based on the hydraulic resistance net. The involved plant structural information are also at organ level. The biomass produced by leaf photosynthesis (source) is transported into different types of organs according to their sink strength, which conceptually describes the requirement of photosynthetic biomass for certain part of plant[6, 7]. Biomass is assumed to be composed of carbohydrates (dry matter) and water respectively at 20% and 80%. Other components containing N, P, K, participate only to the plant functioning, but are negligible for Biomass participation.

Plant sink has been investigated in three different levels: the crop scale[8], the individual plant organ scale[9], and the molecule scale[10, 11]. In the crop level, biomass partitioning rule according to sink strength serves as harvest estimation, and the source-sink relationship is roughly considered. In molecule level, the efforts focus on the role of sucrose supply and cleavage in changing sink strength within developing the whole plants. In plant organ level, the organ sink strength determinates the biomass partition, and different models might have different forms. For example, in TOMGRO[12] and TOMSIM[13], sink strength is defined as the organ potential growth rate (in $\text{g MS m}^{-2}\text{j}^{-1}$), while in GreenLab organ sink strength is defined as a relative value (has no unit) indicating the capacity of biomass partitioning. Thus the biomass going to an organ is proportional to its sink strength divide by the sum of the active sinks in the plant structure. In TOMGRO, the definition of sink strength facilitates the implementation of centralistic partition concept. There exists a biomass conservation pool when biomass supply exceeds demand [14]. In GreenLab the sink strength varies in the organ lifetime and the variation complies with some expansion law. All the biomass produced in a cycle is distributed into the plant organs.

The fruits are the major sinks in fruit trees or fruit vegetables [15]. The leaves are both sources and sinks organs. The biomass distributed into leaves assures the expansion in leaf area. The feedback of plant topological and geometrical information on biomass production and partition during the plant growth process helps to precisely calculate the hydraulic resistance net, and in consequence the photosynthesis increases with leaf expansion or decreases with leaf senescence. The process is simulated by the GreenLab mathematical engine, as enables us to formulate the methodology to find the optimal plant fruit sink strength with respect to the calculated fruit weight based on the model calibrations for wheat [16], maize, cotton and sunflower, etc. In this paper we illustrate the methodology in the case of maize. According to the results of this paper we can tell, in the sense of optimal fruit sink strength, the maize growing in the field is optimal or not. We name this optimal sink strength the sink reference.

2 The Description of Plant Source–Sink Relationships Optimization Problem

2.1 GreenLab model[9]

GreenLab is a plant functional-structural model under a set of biological assumptions from botany and crop physiology. The sum of temperature effect and linear water transpiration assumption serve as the plant phenological and trophic processes respectively.

Two aspects of phenology, the temporal and topological organization are considered to describe the plant development and differentiation. The temporal organization is based on the sum of temperature effect which leads to the thermal time index GC, and the phytomers produced during one GC form growth units (GU); the topological organization is based on discrete botanical entities, such as internodes, leaves and flowers.

In each GC, we assume that plant undergoes primary and secondary growth. For the former, fresh biomass is allocated into organs and phytomers are added and lengthened at the beginning of each cycle; during the cycle, fresh biomass is produced according to the water transpiration considering hydraulic resistance of organs (architectural information feedback); for the latter, the ring and fruits are added, and the internode diameters increased at the end of the cycle. The number of the new phytomers is proportional to the sum of the daily average temperature, as is addressed in introduction section.

For trophic process, in a sufficient long period, the fresh matter is linearly related to water transpiration, and the proportionality factor is defined as Water Use Efficiency[9] (WUE). The WUE might vary with respect to region and plant species. The amount of water transpiration depends on physical water flow through the plant hydraulic architecture. The water flow is monitored by a hydraulic potential and the internal hydraulic resistance of the plant hydraulic network. The main hydraulic resistance lies in the leaf surface where the water changes from liquid to vapor and evaporates to the atmosphere through the stomata. The fresh matter fabricated at each GC is formulated as

$$Q_n = \frac{E_n}{R_n}, \quad (1)$$

where Q_n is the biomass production at growth cycle n ; E_n is the average biomass production potential during the growth cycle, which depends on WUE and the environmental factors such as light, temperature and soil water content. R_n is the hydraulic resistance of the plant expressed as the sum of the hydraulic resistances of all the leaves whose number is evaluated at each cycle according to architecture structure of the plant species.

Each organ is assumed to have a direct access for biomass exchange. Leaves, internodes, fruits and layers, root system are sinks for Biomass. All the organs compete for biomass allocation according to their sink strengths. The expansion of leaves in turn introduces retroaction on the biomass production in the next growth cycle.

To simulate the biomass production in cycles and construct the plant architecture, 13 parameters, namely the organ sink strengths, the organs allometry, their expansion laws, the seed volume and the resistivities, are sufficient for GreenLab. It is the first time that under a simple set of assumptions the evolution of the organ sizes along the architectural profile of the plant is fully simulated.

Formulas for partition of fresh matter

The demand of biomass at cycle n is

$$D(n) = \sum_{o \in \{a, e, c, f\}} p_o \sum_{i=1}^{t_o} \phi_o(i) N_o(n-i+1), \quad (2)$$

where $o \in \{a, e, c, f\}$ represent leaves, internodes, rings and fruits or flowers respectively, p_o is the sink strength of o -type organ which is a relative value, $\phi_o(i)$ is the sink variation during the expansion law of o -type organs when they are i -cycles-old, t_o is expansion duration of o -type organ, $N_o(i)$ is the number of o -type organs in i cycle.

The biomass allocated of o -type organ grows for t cycle at n cycle is:

$$\Delta q_o(t, n) = \frac{p_o \phi_o(t)}{D(n)} Q(n-1), \quad (3)$$

Formulae for fresh biomass production

According to the flow network of the leaves the resistance of one leaf at cycle n is as follows

$$R(n) = \frac{r_1}{S(n)} + r_2, \quad (4)$$

where $S(n)$ is the surface of leaf at cycle n , r_1 is the resistivity of blade, and r_2 is the resistivity of petiole, then considering the architecture of plant, the Equation (1) becomes [3]

$$Q(n) = E \sum_{i=1}^{T_a} \frac{N_a(n-i+1) \sum_{j=1}^i \frac{\phi_a(j) Q(n-(i-j)-1)}{D(n-(i-j))}}{A_n + B \sum_{j=1}^i \frac{\phi_a(j) Q(n-(i-j)-1)}{D(n-(i-j))}}. \quad (5)$$

where A_n, B are parameter compositions of leaf resistivities and sinks, T_a is the leaf work time, $Q(n)$ is the fresh biomass produced at cycle n .

2.2 Fruit weight calculation [3]

For optimization the objectives must be specified. It's natural to choose fruit weight as the cost function. The fruit weight can be calculated as follows

Let $N_f(n)$ be the number of the fruits at cycle n which have an sink strength p_f , and a expansion law $\phi_f(i)$ for several cycles, let T_f be the cycle at which the fruit appear, we have

$$\text{If } n \leq T_f, \quad p_a(n) = \frac{p_a}{p_a + p_e}, p_e(n) = \frac{p_e}{p_a + p_e}, p_f(n) = 0$$

If $n > T_f$,

$$p_a(n) = \frac{p_a}{p_a + p_e + p_f}, p_e(n) = \frac{p_e}{p_a + p_e + p_f}, p_f(n) = \frac{p_f}{p_a + p_e + p_f}$$

The visible fruit at cycle n is built at the end of cycle $n-1$, and share the fresh biomass with the internodes and leaves built at cycle n . The demand Equation (2) now can be specified as

$$\begin{aligned}
D(n-(i-j)) = & \sum_{k=1}^{t_a} \{p_a(n-(i-j)-k+1)N_a(n-(i-j)-k+1)\phi_a(k)\} + \dots \\
& + \sum_{k=1}^{t_e} \{p_e(n-(i-j)-k+1)N_e(n-(i-j)-k+1)\phi_e(k)\} + \dots \\
& + \sum_{k=1}^{t_f} \{p_f(n-(i-j)-k)N_f(n-(i-j)-k)\phi_f(k)\}
\end{aligned} \quad (6)$$

substitute new demand Formula (6) to the GreenLab Equation (5), now we point out that in (5)

$$A_n = \frac{er_1}{p_a(n)}, \quad B = r_2$$

where e is the leaf thickness. The weight of fruit at cycle n which appeared at cycle $n-i+1$ is formulized as

$$q_f(n-i+1, n-1) = p_f \sum_{j=1}^i \frac{\phi_f(j)Q(n-(i-j)-1)}{D(n-(i-j)-1)}. \quad (7)$$

2.3 Calibration results for maize

Calibration experiments are conducted in China Agriculture University (CAU) with sufficient fertilizer and water. The maize is well protected from pests and diseases; row and column spacing are distant enough to prevent competitions between maize individuals. Some parameters are calibrated by data fit of the measure data directly, and others are determined by least square method. For maize, there is no layer, no petiole but sheath for the leaves, the female flower grows to be a cob. Calibrated parameters are loaded into testfile maize.m, and most of them are listed: in Fig.1.

Topology	- Leaf expansion duration: 8 cycles
- maximum number of internodes: 22	- Blade thickness: 0.0283 g/cm ²
- leaf position: 1 – 22 internodes	- Resistivity: $r_1=38000$ (for blade),
- female flower position: 16 th internode	$r_2 = 0$ (for sheath)
- male flower position: 22 th internode	- Sink strengths (no unit): pb = 1.0
- one leaf per node	(blade); pp = 0.666 (petiole); pe = 1.89
	(internode); pc = 0; pf (female flower
	or fruit) = 201; pm(male flower) =
Functioning	1.49;
- Age of growth in cycle: 30	- Organ expansion parameters are
- Seed volume: 1.0 g	calibrated too.
- Leaf work time T_a : 12 cycles	

Fig.1 Maize simulation at different fruit sink strength

3 Maize Optimal Sink Strength Solution

3.1 Maize growth simulation at different sink strengths

We can see in Equation (2), (3), the biomass partition among different organs is dramatically influenced by their sink strengths. From the calibration results, the sink

strength of female flower (fruit) is extraordinarily bigger than the ones of the other organs. The change of fruit sink strength can therefore affect the maize growth profoundly. Now we mathematically let the fruit sink strength p_f range from 10 to 3000 with an increment of 10, the other parameters stay the same as the calibrated ones, and the fruit weight with respect to different fruit sink strength is as Fig.2

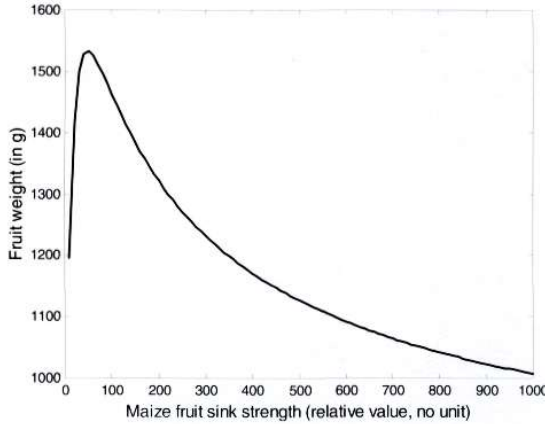


Fig.2 Simulation for different maize fruit sink strength

3.2 An optimal fruit sink strength

Considering the results of Fig.2, one may wonder if there exists an optimal fruit sink strength for the maximal fruit weight, and if it is possible to modify the fruit sink strength to increase the fruit production. Suppose that fruit sink strength changes from a relatively small strength, obviously the augment of fruit sink strength makes more fresh biomass flow into fruits, and consequently fruit weight increase. When fruit sink strength increasing, the biomass allocated to leaves diminishes accordingly, which lessens the photosynthesis and conversely a decrease of the total maize fresh biomass produced at the growth cycle, consequently the fruit weight reduces. Suppose that with positively infinite fruit sink strength, thus no fresh biomass in leaves, and maize stops growing. As a result the fruit weight is zero in this case. Therefore mathematically speaking there is an optimal fruit sink strength which maximizes the fruit production, and it makes sense according to the fresh biomass partition rules of GreenLab.

3.3 Mathematical solution for the maize sink strength static optimization problem

Static optimization is the minimization or maximization of an objective function $f(x)$ in Euclidean n -space subject to constraints on its variables. Suppose there are m constraint conditions, the optimization problem then can be depicted as the following general form

$$\begin{aligned}
 & \min_{x \in R^n} f(x) \\
 & c_i(x) = 0, i = 1, \dots, m_e \quad , \\
 & c_j(x) \leq 0, j = m_e + 1, \dots, m
 \end{aligned} \tag{8}$$

The set of points satisfying all the constraints is named by feasible region.

Now we rewrite the fruit sink optimization problem in optimization content as follows.

$$\min_{x \in R} f(x) = \text{simu_grow}(x, \Omega), \quad 0 < x < 3000 \quad (9)$$

where x is the fruit sink strength chosen as optimization variable and subject to a bound constraint, Ω is the GreenLab parameter set the certain species of maize in CAU, and the objective function simu_grow , in which in fact GreenLab code is embedded, calculates the fruit weight according to Equation (7) where $n = 30$ and $n - i + 1 = 16$ from the calibration results. This Equation (9) can be catalogued into bounded nonlinear optimization problem, and can be solved by numerical methods [17]. In this paper we apply Matlab optimization toolbox, since at the moment GreenLab is implemented in Matlab.

The optimal fruit sink strength is 47.5, and the optimal fruit weight is 1533g. We also simulate maize growing with parameters calibrated by CAU data, in which fruit sink strength is 201, and the fruit weight is 1320g. Fig.3 shows the difference between the optimal fruit sink strength and calibrated sink strength simulations. And the biomasses allocated into different organs are compared in Fig.4.

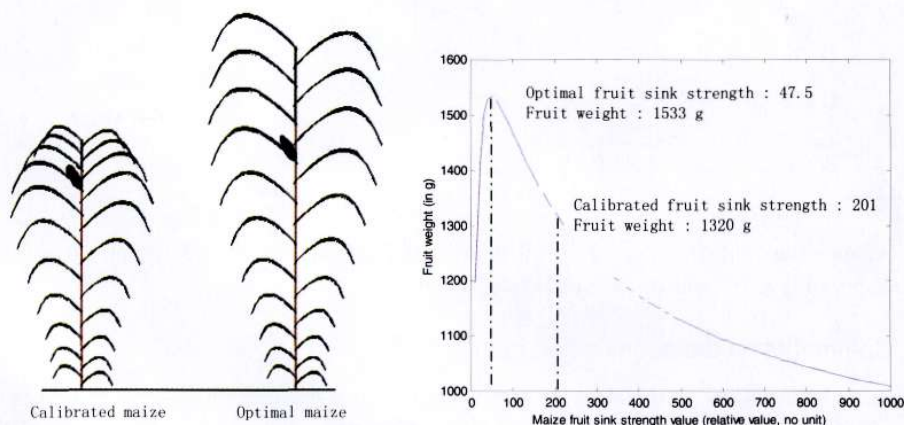


Fig.3 Comparison of 3D simulation results and fruit weight between the optimal maize with the fruit appearing at the 16th internode and the calibrated one

For the fruit appears at growth cycle 16 and functions for one cycle, the fruit optimal growth can be 16% heavier than the maize which grows in the CAU experiment. Now at every possible position of fruit, we optimize the fruit sink strength as above, and we list the results in the right of Fig.5, including the results for the maize with fruit appearing at the 16th internode. The optimal fruit appearance position is at 20 growth cycle (suppose that there is at least two internodes between male and female flowers), the accordingly optimal fruit sink strength is 311 and optimal fruit weight is 1931 g which is 46% heavier than the maize which grows in the CAU experiment, as is shown in Fig.5.

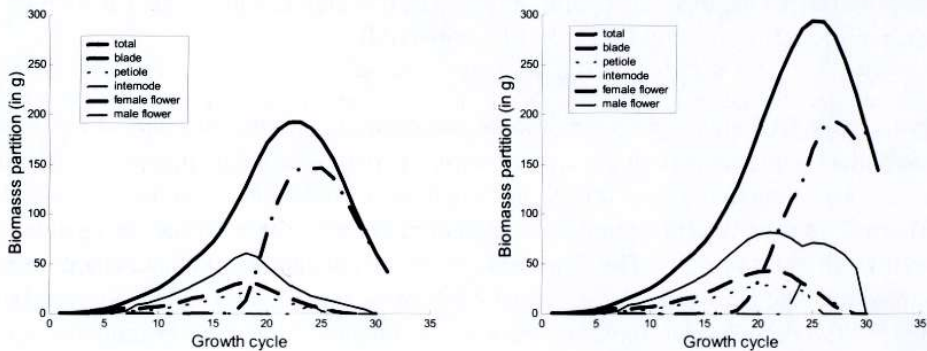


Fig.4 Comparison of biomass production and partition between the optimal maize with the fruit appearing at 16th internode (right) and calibrated one (left)

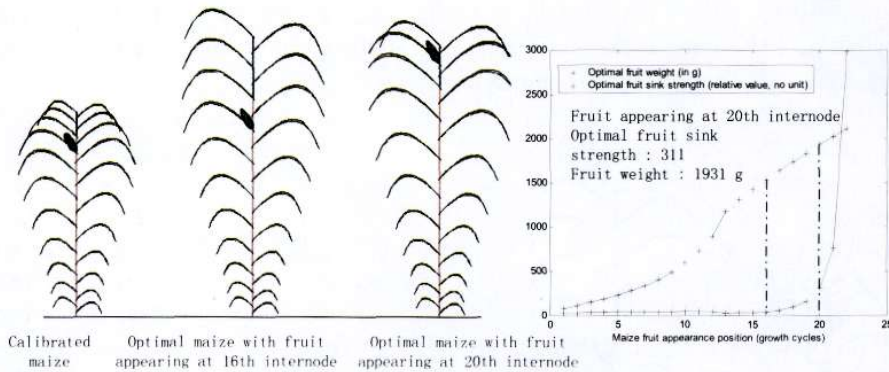


Fig.5 Comparison of different maize growth between the calibrated maize and the optimal ones with the fruit appearing at 16th and 20th internode respectively

3.4 Comments on the optimization results

As Zhan points out[16], in the early growth stage the sink strength ratio between leaves and internodes can be various, but after the ratio keeps nearly constant. The appearance of fruit changes the partition of biomass profoundly. The sink strength of certain organ indicates its power of absorbency, and can be considered as a genetic factor of maize.

The fruit sink strength optimization results are interesting in the theoretical point of view for agronomy. As indicated in Fig.2, for certain maize species we can tell it is an optimal one or not, and compare its position in the Fig.5 with the theoretical optimal sink reference. And furthermore, certain species of maize with high fruit sink strength and less fruit production becomes valuable, when hybridizing it with a relatively vegetative maize to diminish its fruit sink strength, so that the new hybridized one can approach to the calculated optimal reference. If the computed sink strength of the observed plant is on the right of the optimal one, the optimal plant will have the drawback to produce more biomass to fulfill it. So the plant will need more water and fertilizers. Economically speaking it may be not interesting and another economical constraint has to be introduced. On the other hand in a left position the gain is obvious. That's to say, a macroscopical direction at the organ

level is drawn in the sense of GreenLab for the plant that can guide the research at the genetic molecular level.

Here we point out that the optimal reference depends on the form of objective function, which can also be the fruit shape or other forms. The optimization in this paper is in fact a one-factor analysis process, therefore the results also depend on the other internal or external parameters, which at the moment we assume to be nearly the same for all species of maize.

The concept of optimal reference can be extended to multi-factor analysis by choosing the genetic plant parameters which are evaluated to have important impacts on plant growth in the future work. The extended reference can be considered as the GreenLab criteria for different species of maize.

4 Discussion

In this paper we present the methodology for the plant optimization source-sink relationships based on a plant functional-structural model. This paper shows obviously the importance of the feedback between plant structure and plant functioning. The source – sink relationships are continuously changing according to the plant phenology. So the biomass acquisition and the biomass partition are modified at each growth cycle. According to Plant breeding or plant cultivation it is possible to modify the sink strength or the organ functioning period. The model can predict the gain or the sensibility for each parameter optimization. The theoretically optimal fruit sink reference can be obtained to act as a criterion of the plant in the field. We show the application of the methodology in the case of maize, and it can also be extended to other cases such as wheat, cotton, etc. The fruit sink strength and fruit appearance position have significant influence on plant growth according to the simulation results of GreenLab, and the fruit sink reference can then be achieved using numerical optimization algorithms. The numerical algorithms are valid for all their corresponding optimization problem type, independent of plant model. The experience of numerical optimization on GreenLab can therefore be extended to other plant models.

Model-based plant optimization is one of the applications of model itself; it cannot optimize what the model cannot yet describe. Conversely the novelties of model-based optimization depend on the objectives, characteristics of plant model. The optimal fruit sink results benefit from the functional-structural characteristics of GreenLab model. However the results are preliminary and can be refined considering the maize-related aspects, since GreenLab is a generic plant model and does not integrate precise maize background. But it shows the importance of the feedback between plant architecture and plant functioning whatever are the factors involved in the functioning itself.

(1) The environmental factors, such as soil nitrogen content and radiation, are not specified in the biomass production potential E_n , we use the average biomass production potential E_n for each growth cycle to roughly describe the environmental factors. For practical application in field, these environmental factors are important for the maize grain filling.

(2) In field crop research, Rajcan and Tollenaar[18, 19] conducted a 3-year experiment for two maize hybrids, Pride 5 and Pioneer 3902, and concluded that the larger source-sink ratio is associated with the increase of leaf longevity and the greater dry matter accumulation is associated with leaf longevity. The leaf longevity was enhanced by an increase in soil N, and the proportion of in the grain derived from post-silking N uptake was

positively associated with the source-sink ratio. In GreenLab the span of the leaf functioning time " T_a " is of course a key factor. The model can compute the increasing of the yield resulting from an increase of T_a . This one can be modify upon fertilizer or plant breeding.

(3) For maize, leaf extension is almost finished before there is a significant mass increment in the cob. Therefore in the case of maize, the competition for biomass between leaves and fruits is slight (Fig.4).

The model will become much more complex when incorporating these features of maize, as would arise the complexity of optimization problems, and the optimization algorithms would become more complex accordingly.

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